Introduction

Understanding of the distribution and abundance of many populations of offshore cetaceans is limited because of the difficulty and expense of obtaining quantitative estimates of these parameters (Hammond, 2010). Surveys of such populations typically occur at very broad spatial scales, interspersed by long time periods (e.g. Hammond et al., 2002, 2013; Gerrodette and Forcada, 2005). Thus, there is often a spatial mismatch between available data and information needed to assess the potential impact of human activities on pelagic cetaceans in specific areas. In addition, the snapshots of cetacean occurrence and density from broad-scale surveys provide no information on potential seasonal trends in these parameters.

This paper reports the results of an intensive three-year study of the occurrence, distribution and abundance of cetaceans in Onslow Bay, North Carolina, USA, within the South Atlantic Bight. In 2005, the US Navy proposed development of an Undersea Warfare Training Range (USWTR) in this area (Department of the Navy, 2009). Relatively little was known regarding the occurrence of cetaceans in the offshore waters of Onslow Bay because most previous surveys in the South Atlantic Bight had been conducted at a very coarse spatial scale (Mullin and Fulling 2003; Garrison et al. 2010). To address this data limitation, an intensive survey programme was begun in June 2007. In 2009, the Navy changed its preferred site for the USWTR to an area off Jacksonville, Florida (Department of the Navy, 2009), but our surveys continued in Onslow Bay.

The proposed USWTR in Onslow Bay consisted of an area of 1,715km² that straddled the 200m isobath (Fig. 1). A variety of cetaceans were known or believed to occur in this area, including shelf-associated species such as Atlantic spotted dolphins (Stenella frontalis) and common bottlenose dolphins (Tursiops truncatus) and pelagic species, such as short-finned pilot whales (Globicephala macrorhynchus) (Mullin and Fulling, 2003; Garrison et al., 2010). In addition, several mysticetes, such as endangered North Atlantic right whales (Eubalaena glacialis), likely use portions of Onslow Bay as a migratory corridor (Schick et al., 2009).

A monitoring plan was developed that included monthly aerial and shipboard surveys for cetaceans and sea turtles, strip-transect surveys for seabirds and passive acoustic monitoring of cetaceans with a towed hydrophone array and a series of moored recorders. The results of three years of aerial and shipboard line-transect surveys for cetaceans, beginning in June 2007 are reported in this paper. The results of the passive acoustic monitoring programme (Hodge, 2011) and sea turtle and seabird surveys (Thorne, 2010) will be reported separately. A suite of complementary field methods (aerial surveys, vessel surveys and passive acoustics) deliberately selected to maximise the probability of detecting all cetaceans in the study area, including deep-diving and cryptic species (Barlow, 1999). To extend the time...
series and increase the sample size of observations, an earlier series of aerial surveys conducted in this area in 1998 and 1999 was also incorporated.

The objective of the research, therefore, to provide a comprehensive description of the occurrence, distribution and abundance of cetaceans in Onslow Bay, including seasonal variation in these parameters.

METHODS

Study area

The proposed USWTR site in Onslow Bay consisted of a rectangle 46 × 37km; the center of this rectangle is approximately 90km from shore. Surveys extended beyond the proposed boundaries of the USWTR, so the total prediction area was 5,334km². Surveys were conducted along ten transect lines that were placed perpendicular to the coast and the shelf break, each 74km in length and spaced approximately 9km apart, in this area (Fig. 1). Both aerial and vessel surveys used the same set of tracklines.

The dominant oceanographic feature of the study area is the Gulf Stream, which meanders back and forth over the shelf break as it flows northwards. As a result of these meanders, oceanographic conditions at any point in the study area can vary considerably in only a few days. The 200m isobath bisects the study area (Fig. 1) which, therefore, included both the continental shelf and slope waters.

Aerial surveys

Aerial surveys were conducted from June 2007 to June 2010 inclusive in a Cessna 337 Skymaster at an altitude of 305m and a speed of 185km hr⁻¹. Surveys were conducted on days with low sea states (Beaufort 0–3) and optimal visibility. The goal was to complete a full set of ten tracklines twice each month. The earlier set of aerial surveys was conducted over a slightly different set of tracklines in the same location from September 1998 to July 1999, also using a Cessna 337 and a similar survey protocol, except that the plane flew at 230m (McLellan et al., 1999). Sightings data from the two sets of aerial surveys were combined. To improve precision of the detection functions of certain species, sightings from aerial surveys for right whales conducted closer to shore by the University of North Carolina Wilmington were also incorporated (all survey results reported in OBIS-SEAMAP; Halpin et al., 2009).

During aerial surveys, an observer monitored each side of the plane, equipped with a GPS unit, data sheet and binoculars; each side was considered to be an independent transect. The observers recorded the start and end of transect lines, any changes in environmental variables (i.e. cloud cover, sea state, visibility and glare) and sightings of marine mammals, sea turtles and vessels. When a sighting cue was observed, the observers estimated horizontal and vertical sighting angles by eye. The aircraft then broke from the trackline and closed on the sighting location. The plane circled over the sighting to obtain photographs to confirm species identity. During each encounter, the left observer was designated as data recorder and the right observer obtained digital photographs with a Canon 40D camera and a 100–400mm image-stabilised lens. These images were used to assist with species identification (see below), refine estimates of group size and confirm sightings of calves. A best estimate of group size was established using both field observations.
4.2m above waterline for the vessel surveys. During winters, lower targets of monthly survey effort were set due to seasonal variation in sea conditions. The target of survey effort varied over the course of the study, with a maximum goal of five transects per month during the summers of 2007 and 2008. Due to seasonal variation in sea conditions, lower targets of monthly survey effort were set during winters.

Observations were made from the flying bridge (5.0m and 4.2m above waterline for the Sensation and Cetus, respectively) using naked eye and 7 x 50 binoculars. While on effort, two observers (one port and one starboard) scanned constantly from straight ahead to 90° abeam either side of the trackline. A third observer monitored the trackline, coordinated with the vessel skipper and acted as data recorder. The observers rotated positions (including at least one rest station) every 30 minutes. Survey speed was approximately 18km hr⁻¹. Standard line transect sampling methods for cetaceans were used, similar to those described by Barlow (2006).

The location and species identity of each cetacean group were recorded. Each observer estimated group size independently and these estimates were averaged at the end of each survey to generate a final estimate of group size. Environmental conditions (weather, sea state, depth and sea surface temperature) were recorded every 30 minutes or whenever sighting conditions changed. All sighting and environmental observations were entered into an onboard data collection system (Vis-Survey, developed by Dr. Lance Garrison, NOAA SEFSC Miami, FL) linked to a GPS unit.

During these vessel surveys a hydrophone array (Seiche Instruments, UK) was towed approximately 150m behind the vessel. The array consisted of four elements, spaced 1.2m apart, with a flat (+/− 3dB) frequency response between 2 and 100kHz and a sensitivity of −165dB re 1V/μPa. High-frequency acoustic recordings at 192-kHz sampling rate were made on a laptop running Ishmael software (Mellinger, 2001) and a MOTU Traveler audio interface (Mark of the Unicorn, Cambridge, MA, USA). A trained acoustician monitored incoming acoustic signals aurally and visually via spectrograms in Ishmael, with the gain set to −96dB.

Recordings were made directly to an external hard drive whenever calls were detected using Ishmael, at which point time and location were noted. The recording station was located in the main cabin of the survey vessel, isolated from the visual observers, so the acoustic and visual surveys functioned independently.

In addition, patterns of residency in the study area were monitored by identifying individual animals using photo-identification techniques. Thus, whenever possible, digital photographs were obtained for photo-identification. These photographs were also used to confirm species identification and to compare identification features with those used by the aerial survey team (see below). Canon or Nikon digital SLRs equipped with 100–300mm zoom lenses were used. All photo-identification images were graded for quality and individual distinctiveness using methods described in Read et al. (2003).

Species identification
Digital images of each sighting were reviewed in the laboratory to confirm species identity. During the first year aerial and shipboard observers reviewed every sighting together and established a set of diagnostic features that were subsequently used to identify each cetacean species. Common bottlenose and Atlantic spotted dolphins were sometimes difficult to distinguish from the air, particularly when groups were comprised entirely of juveniles. In addition, it is difficult to differentiate short- and long-finned species of pilot whales (G. macrocephalus and G. melas, respectively) at sea (Rone and Pace, 2012). Thus, if species identity could not be unequivocally determined, the sighting was designated to the nearest taxonomic category (e.g. ‘unidentified delphinid’).

Statistical analysis
General approach
To generate density surfaces and, where possible, identify environmental variables driving patterns of animal distribution, the probability of detection associated with each sighting was estimated and then surface density per segment of trackline within the truncation distance was estimated. Detection probabilities were estimated assuming that detection of an animal on the trackline was certain (see below for a discussion of this assumption).

The survey region is heterogeneous with substantial changes in depth and the fluctuating presence of the Gulf Stream. The adjusted density data were characterised by a high ratio of zero to non-zero segments, so density was modelled with a two-stage process: (1) the probability of presence as a logistic generalised additive model (GAM); and, (2) estimated density, given that animals were present. The product of these two prediction surfaces gave an estimated relative density surface for the study area. Abundance was then obtained by numerically integrating over these surfaces. The resulting abundances do not take into account periods when animals were submerged, and therefore unavailable for detection, or imperfect detection on the trackline. Due to limited sample sizes, only bottlenose dolphins and Atlantic spotted dolphins could be modelled.

Estimation of detection probabilities
Either a hazard-rate (1 − exp(− y/σ)⁻¹) or half-normal form (exp(− y²/2σ²)) was used for the probability detection function (σ is the scale parameter) (Buckland et al., 2001) where y is perpendicular distance. The effects of covariates, other than perpendicular distance were incorporated, into the detection function model by setting the scale parameter to be an exponential function of the covariates (Marques, 2001). Thus, the probability of detection becomes a
multivariate function, \( g(y,v) \), representing the probability of detection at perpendicular distance \( y \) and covariates \( v \) \( (v = v_1,..,v_Q) \) where \( Q \) is the number of covariates). The scale term, \( \sigma \), has the form:

\[
\sigma_i = \exp \left( \beta_0 + \sum_{q=1}^{Q} \beta_q v_{iq} \right)
\]

and \( \beta_0 \) and \( \beta_q \) \( (q = 1,..,Q) \) are parameters to be estimated. With this formulation, it was assumed that the covariates may affect the rate at which detection probability decreases as a function of distance, but not the shape of the detection function. In the aerial case the covariates considered were Altitude, Beaufort Sea State and Glare. In the boat case, the covariates were Species, Beaufort Sea State, Group Size and Visibility.

A backward, stepwise selection procedure (starting from the previous best model) was used to decide which covariates to include, with a minimum Akaike’s Information Criterion (AIC) inclusion criterion. All initial model selection was performed in the program Distance (v5.0; Thomas et al., 2002) and re-fitted the final selected models using a set of customised functions (mrds v.1.3.8) in R 2.9.2 (R Developmental Core Team, 2009). This facilitated estimation of variance within \( R \) (see below).

In general, rates of encounter rates with cetaceans were very low during the 2007–10 surveys, so detection probabilities were estimated by augmenting sightings with data gathered from the same aerial platform during surveys carried out closer to the coast and another set flown near Wallops Island, Virginia in 1998 and 1999 (McLellan et al., 1999). Additional shipboard sightings were also incorporated, using the same methodology and observers, from the F/V Sensation obtained during a brief survey off Cape Hatteras, where cetacean densities are much higher, in 2007. All dolphin species were grouped into a single guild of delphinids to estimate detection functions and then evaluated species as a covariate when fitting the detection function. There were too few sightings to estimate density for species other than bottlenose and spotted dolphins.

Estimation of density surfaces

A modified version of the ‘count model’ of Hedley et al., (1999) was implemented to model spatial distribution. The response variable for this model was a density based on the estimated number of individuals for a small segment \( i \) of trackline, \( \hat{N}_i \) calculated using an estimator similar to the Horvitz-Thompson estimator (Horvitz and Thompson, 1952), as follows:

\[
\hat{N}_i = \sum_{j=1}^{6} \frac{s_j}{\int_{y} g(y,v_j)\pi(y)dy}, \quad i = 1,..,T,
\]

where, for segment \( i \), \( \int_{y} g(y,v_j)\pi(y)dy \) is the estimated probability of detection of the \( j \)th detected pod, \( n_i \) is the number of detected pods in the segment and \( s_j \) is the size of the \( j \)th pod. The total number of transect segments is denoted by \( T \). By assumption, \( \pi(y) \) the probability density function of actual (not necessarily observed) perpendicular distances is uniform up to the truncation distance; this is satisfied by locating transects randomly.

Having obtained the estimated number of individuals in each segment, the density in segment \( i \), \( \hat{D}_i \), from \( \hat{N}_i/a_i \) where \( a_i \) is the area of segment \( i \) was estimated. Segment area was calculated as the length of the segment multiplied by twice the truncation distance used to model the detection function. The survey tracklines were initially divided into distinct segments based on effort and sighting conditions. Long segments were divided and a variety of segment lengths from 5 to 13km were evaluated; 10km was chosen as an appropriate compromise between maximising the ratio of non-zero to zero segments, maintaining environmental resolution and giving some measure of spatial independence (see Results).

In most cases, the number of segments with detections was extremely low, which made fitting of models difficult, so a variety of alternative approaches were explored. Zero-inflated methods were investigated, but these proved impossible to implement successfully with the dataset. Therefore, a two-stage process was implemented: the presence or absence of animals in a particular segment was modelled using a logistic GAM and then non-zero density was modelled in each segment again with a GAM but now assuming a Gamma error structure. The predicted probability of the presence of animals in a segment was multiplied by the predicted non-zero density in that segment to obtain the predicted density of animals. This two-stage process may introduce a potential bias in that absences (zeros) are over-represented because some observed zeros were not true absences, but simply segments of low density where animals were present but not observed. Perfect correction for under detection is not possible given the absence of a \( g(0) \) estimate.

The following covariates were included in the models: sea surface temperature (Temp); depth (Depth); day of year (Dayofyear); and year of survey (Year). Dayofyear was considered as a cyclic cubic spline, so the second derivative of the curve for Dayofyear met at the beginning and end of the year. Sea surface temperatures were collected during shipboard surveys, but for the aerial survey and prediction grid temperatures were obtained from ETOP02 at 2-minute resolution. Year was trusted as a factor rather than a continuous variable because of the break in surveys between 1999 and 2007.

Temperatures and depths were associated with effort segments by finding the closest point in the temperature and bathymetry data to the midpoint of the effort segments using great circle distances (and date for temperature). Finally, Survey was incorporated as a factor to identify the survey platform (plane or boat), but only if the estimated value of the regression coefficient associated with the plane was lower than those associated with the ships, i.e. the use of Survey reflected differences in \( g(0) \) between aerial and shipboard surveys.

Backwards model selection was implemented using generalised cross validation (gcv) in the mgcv package (v. 1.5–2) in R (v. 2.9.2) for covariate selection in the logistic model, augmented with diagnostic plots, using the principles described in Wood (2006). Model selection was by

\[^{6}\text{http://dss.ucar.edu/datasets/ds277.0/data/oiv2/}.
\[^{7}\text{http://www.ngdc.noaa.gov/mgg/image/2minrelief.html.}\]
generalised cross validation. All covariates were considered for inclusion in the model as 1D smooths of untransformed covariate values. A maximum of four degrees of freedom was allowed in the selection of 1D smooths for Temp, Depth and Dayofyear as the response to these variables would be unlikely to have more than two minima and maxima. The presence of unexplained spatial variation was looked for by inspection of semi-variograms of the residuals of the models. Models were fitted to all data across all years. Survey was included in all models to account for the detectability differences on the trackline between aerial and ship surveys. Due to variation in environmental conditions along transects, it was not always split survey effort into segments of equal length (see below). Therefore, the model was weighted by segment area. The presence-only data were modelled in the same way, although sometimes simplified models were chosen for the point estimate to avoid generating spuriously high results in the bootstrap where the full range of data might not be available, leading to dubious extrapolation over the entire prediction region.

Prediction of density and variance estimation
The final models were used to predict density using a two-minute resolution prediction grid. Abundance was estimated by numerically integrating under this predicted density surface. If survey platform was included in the final model, abundance was predicted assuming the survey mode with the largest coefficient value, as this would reflect the best detection on the trackline. Predictions were made for every month of each survey year to allow comparison of seasonal trends across years.

Variance was estimated by repeating the entire abundance estimation process on a large number of samples, drawn at random from the data, to obtain a distribution of abundance estimates. Confidence intervals were derived from this distribution using the 2.5% and 97.5% percentiles to obtain the upper and lower limits. Samples were obtained by sampling transects, at random and with replacement, so that the selected effort reflected the effort in the original sample and accounted for evidence of temporal correlation in the residuals by the same sections of effort together being used. Models were refitted with the same covariates as in the original analysis but the degrees of freedom available to each were reselected, subject to the constraints mentioned above.

RESULTS
Aerial surveys
Aerial surveys of all tracklines were conducted each month from June 2007 to June 2010, with the exception of January and September 2008 and May 2010. The aerial survey covered 42,676km of trackline, with most (78%) effort occurring in Beaufort Sea States 2 and 3. An additional 12,821km of trackline were flown between September 1998 and July 1999, with effort in every month except February 1999. Taking both data sets together, 55,497km of trackline were surveyed with effort in every calendar month.

A total of 279 sightings of seven species were recorded during these aerial surveys. Atlantic spotted and common bottlenose dolphins dominated the cetacean fauna (Table 1). The sightings included 22 unidentified delphinid schools and an observation of a single group of unidentified beaked whales in May 1999. In addition, an off-effort sighting of a single sperm whale (Physeter macrocephalus) was recorded while transiting to the offshore end of a trackline in October 2009. No mixed-species groups were observed. Species composition was similar in the 1998–99 and 2007–10 surveys, with two exceptions. No spotted dolphins were observed during the earlier surveys, but this species comprised more than a quarter of all sightings in the latter period. In contrast, common dolphins (Delphinus delphis) were observed in the earlier time period but not the more recent surveys. Based on the distribution of long- and short-finned pilot whales during summer (Waring et al., 2011), it is likely that all pilot whales observed from June–August were Globicephala macrocephalus, but it was not possible to confirm species identity of pilot whales during these surveys.

Spotted and bottlenose dolphins were present throughout the year (Table 2). Sightings of bottlenose dolphins were recorded during every month, and sightings of spotted dolphins occurred in every month except July and December (Table 2), although this species was observed during vessel surveys in July (see below). There were too few sightings of other species seen to draw conclusions regarding their seasonal occurrence. Spotted dolphins were restricted to shelf waters; bottlenose dolphins were found over both shelf and deeper waters (Fig. 2a). Pilot whales, Risso’s dolphins, orca, humpback whales and other species were seen occasionally in the area.

Table 1
Summary of cetacean sightings in Onslow Bay, North Carolina, by platform type and period.

<table>
<thead>
<tr>
<th>Species</th>
<th>Aerial surveys</th>
<th>Vessel surveys</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tursiops truncatus</td>
<td>39 (64%)</td>
<td>126 (58%)</td>
</tr>
<tr>
<td>Stenella frontalis</td>
<td>0</td>
<td>57 (26%)</td>
</tr>
<tr>
<td>Delphinus delphis</td>
<td>14 (23%)</td>
<td>1 (&lt;1%)</td>
</tr>
<tr>
<td>Grampus griseus</td>
<td>3 (5%)</td>
<td>4 (2%)</td>
</tr>
<tr>
<td>Globicephala spp.</td>
<td>1 (2%)</td>
<td>7 (3%)</td>
</tr>
<tr>
<td>Steno bredanensis</td>
<td>0</td>
<td>3 (1%)</td>
</tr>
<tr>
<td>Balaenoptera physalus</td>
<td>0</td>
<td>1 (&lt;1%)</td>
</tr>
<tr>
<td>Unidentified delphinid</td>
<td>3 (5%)</td>
<td>19 (9%)</td>
</tr>
<tr>
<td>Unidentified ziphiid</td>
<td>1 (2%)</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>61</td>
<td>218</td>
</tr>
</tbody>
</table>


The sightings included 22 unidentified delphinid schools and an observation of a single group of unidentified beaked whales in May 1999. In addition, an off-effort sighting of a single sperm whale (Physeter macrocephalus) was recorded while transiting to the offshore end of a trackline in October 2009. No mixed-species groups were observed. Species composition was similar in the 1998–99 and 2007–10 surveys, with two exceptions. No spotted dolphins were observed during the earlier surveys, but this species comprised more than a quarter of all sightings in the latter period. In contrast, common dolphins (Delphinus delphis) were observed in the earlier time period but not the more recent surveys. Based on the distribution of long- and short-finned pilot whales during summer (Waring et al., 2011), it is likely that all pilot whales observed from June–August were Globicephala macrocephalus, but it was not possible to confirm species identity of pilot whales during these surveys.

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Vessel surveys
A total of 5,209km of vessel survey effort was recorded from June 2007 to June 2010. Most (70%) of this survey effort was conducted in Beaufort Sea States 2 and 3. A total of 95 sightings of five cetacean species and 5 sightings of unidentified delphinids was made. Species composition (Table 1) and distribution (Fig. 2b) were similar to those observed from the aircraft, with most (87%) sightings composed of common bottlenose and spotted dolphins. Mean group sizes of bottlenose and spotted dolphins were 13.8
Cetacean sightings by month in Onslow Bay, North Carolina, from June 2007 to June 2010. Only aerial survey effort and sightings are presented. Effort is represented by the number of tracklines, indicated in the bottom row.

<table>
<thead>
<tr>
<th>Month</th>
<th>J</th>
<th>F</th>
<th>M</th>
<th>A</th>
<th>M</th>
<th>J</th>
<th>J</th>
<th>A</th>
<th>S</th>
<th>O</th>
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<tbody>
<tr>
<td>Tursiops truncatus</td>
<td>12</td>
<td>5</td>
<td>17</td>
<td>13</td>
<td>14</td>
<td>20</td>
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<td>7</td>
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<td>18</td>
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<td>0</td>
<td>0</td>
<td>0</td>
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<td>0</td>
</tr>
<tr>
<td>Grampus griseus</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
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</tr>
<tr>
<td>Globicephala spp.</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Steno bredanensis</td>
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<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>Balaenoptera physalus</td>
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<td>60</td>
<td>36</td>
<td>60</td>
<td>46</td>
<td>30</td>
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</tbody>
</table>

Table 2

Fig. 2a. Spatial distribution of sightings of cetaceans from aerial surveys in Onslow Bay, June 2007-June 2010. The single sighting of a sperm whale was made off-effort during transit.

Fig. 2b. Spatial distribution of sightings of cetaceans from vessel surveys in Onslow Bay, June 2007–June 2010.

(±1.5) and 22.6 (±5.9), respectively. As was the case for aerial surveys, no mixed-species groups were observed.

The hydrophone array was towed on 41 days, for a total of 194.5 hours of combined visual and acoustic surveys. During these combined surveys a total of 109 acoustic detections of cetaceans were recorded; 68 were visually confirmed and 41 were not observed. Thus, most (62%) acoustic detections of cetaceans were also detected independently by the visual observers.

In total, 3,169 digital photo-identification images of five species of cetaceans were obtained and the following animals were catalogued: 106 individual bottlenose dolphins; 49 spotted dolphins; 16 pilot whales; 12 rough-toothed dolphins; and 7 Risso’s dolphins. Five bottlenose dolphins were resighted: (1) ID 9-016 on 25 July 2008 and 17 August 2009; (2) ID 4-002 on 15 September 2009 and 1 October 2009; (3) 1-004 on 1 October 2009 and 11 April 2010; (4) and (5) IDs 7-015 and 8-009, seen together on 28 April 2009, and seen together again on 20 April 2010. One spotted dolphin, ID 9-013, seen on 9 August 2009 and then again on 1 October 2009 (Fig. 3) was also matched. No individuals of other species were resighted, although the catalogue sizes for these species were small.

**Statistical analysis**

Sightings of all dolphins from aerial surveys were binned into 200m widths because of evidence of rounding and they were right truncated at 1.4km. The best fit dolphin aerial detection function was a hazard rate function including perpendicular distance, Altitude and Beaufort Sea State only.
Vessel sightings of dolphins were binned into 100-m widths and right truncated at 300m. The best fit detection function was a half-normal with Beaufort Sea State as covariate (Fig. 5). The mean aerial detection probability was 0.45 (SE = 0.02). The mean boat detection probability was 0.53 (SE = 0.05).

The tracklines for aerial and shipboard surveys were divided into 7,180 segments (5,873 aerial and 1,307 shipboard). The final fitted models for predicting density and for biological explanation are given in Table 3. Bottlenose dolphins were detected in 174 segments (2.4%). Estimated abundance of this species (rounded to the nearest hundred) varied between 600 (95% CI: 100–1,700, August 2007) and 4,100 (1,300–9,400, May 2010) (Fig. 6). These values correspond to densities of 0.117km–2 (95% CI: 0.016–0.323) in August 2007 and 0.767km–2 (95% CI: 0.238–1.768) in May 2010, respectively. Bottlenose dolphins were encountered most frequently at intermediate depths, with maximal values of presence occurring just off the shelf break (Fig. 7). Abundance varied both across and within years (Fig. 6) with peak occurrence in spring and, to a slightly lesser extent, autumn (Table 2; Figs. 6 and 7). A model assuming uniformity of density in space and time (and a boat survey) produced an abundance of 1,400 (95% CI 700–2,800) equivalent to a density of 0.268km–2 (95% CI: 0.127–0.529).

Spotted dolphins were detected in 78 segments (1%). Given the small numbers detected, estimates of abundance were, unsurprisingly, associated with wide confidence intervals (Fig. 8). Estimated spotted dolphin abundance varied from 0 in 1998–99 to 6,000 (95% CI: 2,500–17,000) in March 2009, which corresponded to a maximum density of 1.122 (95% CI: 0.475–3.182km–2). Spotted dolphins...
exhibited a strong preference for waters over the continental shelf; their presence was not influenced strongly by either temperature or day of year, although both variables were included in the final model (Fig. 9). A model assuming uniformity of density in space and time (and a boat survey) from 2007 inclusive produced an abundance of 1,200 (95% CI 500–1,900) equivalent to a density of 0.230 km$^{-2}$ (95% CI: 0.096–0.364 km$^{-2}$).

**DISCUSSION**

**Occurrence and distribution**

The cetacean fauna observed in Onslow Bay included both shelf and slope-associated species, but was dominated by Atlantic spotted and common bottlenose dolphins. Spotted dolphins were restricted to the continental shelf; bottlenose dolphins were the only species to occur in both shelf and slope habitats (see below). All other species occurred along the shelf break or in deeper slope waters. In total, eight species of cetaceans were observed (including the off-effort sighting of a sperm whale) and one group of unidentified beaked whales. Vessel and aerial surveys produced similar lists of species occurrence in the study area.

Fixed passive acoustic monitoring recorders in Onslow Bay also yielded detections of the calls of pygmy or dwarf sperm whales (*Kogia* spp.), minke whales (*Balaenoptera acutorostrata*) and sei whales (*B. borealis*) (Hodge 2011). Pygmy and dwarf sperm whales are noted for their cryptic behaviour, so it is perhaps not surprising that they were not observed. Despite the frequency with which these two species strand along coasts of the southeastern U.S. (see below) only a very small number of sightings have been recorded during dedicated surveys (Waring et al., 2011). The calls of baleen whales can travel for long distances, so it is likely that the vocalising minke and sei whales occurred outside the area surveyed (Hodge, 2011). North Atlantic right whales were not observed in the study area, although the aerial survey team recorded three sightings of right whales close to shore in November 2007, December 2008 and November 2009 while transiting to the field site.

As had been done by Pyenson (2010), species composition from the surveys was compared with a long-term data set of stranded cetaceans from the ocean beaches of Onslow Bay (Table 4). Bottlenose dolphins dominated the stranding record in Onslow Bay. Six of the eight species observed during the surveys were also represented in the stranding record and the order of frequency was identical for these species in both data sets. A number of pelagic cetaceans were recorded as strandings in Onslow Bay but not observed during the surveys – some of these cetaceans, such as pygmy or dwarf sperm whales, are known to be cryptic (see above), but many others likely occur offshore of the study area. Others, such as humpback whales, *Megaptera novaeangliae* (Swingle et al., 1993; Barco et al., 2002) and harbour porpoises (*Phocoena phocoena*), are coastal species and...
occur well inshore of the study area. In general, there was relatively good concordance between the observations made and the stranding record. The species composition and distribution patterns observed were similar to those recorded during previous broad-scale surveys of the South Atlantic Bight and Mid-Atlantic shelf break (Mullin and Fulling, 2003; Garrison et al., 2010). Surveys did not extend far enough offshore to encounter deep-diving species, such as sperm and beaked whales, on a regular basis, although single sightings of both were recorded at the offshore limit of the study area. The moored passive acoustic monitoring system recorded sperm whale clicks throughout the year in Onslow Bay (Hodge, 2011), although like the calls of baleen whales, these sounds can travel considerable distances. On 20 November 2010 an exploratory aerial survey was conducted further offshore and encountered three groups of *Mesoplodon* spp. along the 1000m isobath. It can be concluded that most beaked and sperm whales in Onslow Bay occur offshore of the boundaries of the study area and this is supported by habitat models for beaked and sperm whales in this area (Best et al., 2012).

### Table 3

<table>
<thead>
<tr>
<th>Model</th>
<th>Terms in model</th>
<th>% deviance explained</th>
<th>Figure</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Tursiops truncatus</em></td>
<td>Logistic component: Survey + s(Depth,4) + s(Temp,3) + Year</td>
<td>4.3</td>
<td>6.7</td>
</tr>
<tr>
<td></td>
<td>Non-zero density component: Survey + s(Depth) + Year</td>
<td>24.6</td>
<td>6</td>
</tr>
<tr>
<td><em>Stenella frontalis</em></td>
<td>Logistic component: Survey + s(Depth,3) + s(Temp,4) + s(Dayofyear,3) + Year</td>
<td>20.2</td>
<td>8.9</td>
</tr>
<tr>
<td></td>
<td>Non-zero density component: Survey + s(Depth,4) + Temp*</td>
<td>36.5</td>
<td>8</td>
</tr>
</tbody>
</table>

*Linear.*

Fig. 7. Relationship between presence/absence of bottlenose dolphins and: (a) depth; and (b) sea surface temperature in Onslow Bay, North Carolina given the other terms in the model assuming a boat survey in 2010. Tick marks on the x-axis represent a datum at that covariate value. Dashed marks represent 2 standard errors lower and upper lines (approximately equal to the 95% confidence interval) associated with the uncertainty in the model only.

Fig. 8. Estimated monthly abundances of Atlantic spotted dolphins (*Stenella frontalis*), with 95% confidence intervals, in Onslow Bay, North Carolina.
It is possible that the bottlenose dolphins observed over the continental shelf included both coastal and pelagic ecotypes (Mead and Potter, 1995). The two forms exhibit fixed genetic differences and probably represent distinct species (Hoelzel et al., 1998); their distribution overlaps on the continental shelf south of Cape Hatteras (Torres et al., 2003). The likelihood of the presence of bottlenose dolphins was greatest near the shelf break, consistent with previous observations of the offshore ecotype (Kenney, 1990). Biopsy samples and detailed photographic records of bottlenose dolphins are being collected so that the distribution of the two ecotypes in this area can be better understood.

The smaller-bodied, offshore form of Atlantic spotted dolphins (Adams and Rosel, 2006) was not observed, although these animals have been seen off Cape Hatteras, North Carolina (A.J. Read, unpublished data). Nor did we encounter several other pelagic species, such as pantropical spotted (Stenella attenuata) or Clymene dolphins (Stenella clymene), which were recorded by Mullin and Fulling, (2003). Like the deep-diving species described above, it is likely that these pelagic species occur beyond the seaward extent of the surveys.

Both bottlenose and spotted dolphins were present year-round in Onslow Bay. Despite some evidence that the probability of their presence was affected by sea surface temperature, no clear seasonal patterns in the abundance of bottlenose dolphins were observed, even though the pelagic ecotype of this species is believed to exhibit seasonal movements along the continental slope (Kenney, 1990). There was some indication of an effect of season and/or water temperature on the probability of the presence of spotted dolphins, but this effect was small compared to the overriding effect of water depth.

Approximately 5% (5 of 106) of well-marked bottlenose dolphins and 2% (1 of 49) of spotted dolphins were resighted, despite limited photographic sampling effort.
These resightings occurred over seasons and years, suggesting some degree of structured habitat use by individual dolphins. We are not aware of any other attempts to match images of Atlantic spotted dolphins and offshore bottlenose dolphins along the US east coast, but these findings suggest that such work could provide insight into the population structure of these species.

There were two noticeable changes in species composition between 1998–99 and 2007–10. Short-beaked common dolphins were the second-most frequently observed species in 1998–99 but were almost entirely replaced by Atlantic spotted dolphins in the more recent surveys. Only one sighting of common dolphins in 2007–2010, on 9 March, were spotted dolphins in the more recent surveys. Only one species, but only three of these sightings were recorded during the more recent surveys. It is also possible that the increase in spotted dolphin abundance (see below) over the study period represents a population incursion from more southern waters.

**Abundance**

The abundance of cetaceans in Onslow Bay was very low, although the data were inadequate to estimate density for species other than Atlantic spotted and bottlenose dolphins. A relatively small number of groups of these two species were encountered, resulting in wide confidence limits around the estimates (Figs. 6 and 8) and limiting the inferences that can be drawn from changes in abundance over time.

In general, the estimates of density of spotted and bottlenose dolphins are comparable with those of Mullin and Fulling (2003), who surveyed a much larger area. Atlantic spotted dolphins and bottlenose dolphins were the two most abundant species observed by these researchers, although their survey included an extensive area of pelagic habitat where coastal Atlantic spotted dolphins do not occur.

Like those of Mullin and Fulling (2003), the estimates of density presented here are negatively biased to some degree because it was not possible to meet the assumption that all groups of cetaceans on the trackline were detected (i.e. that $g(0) = 1$). Some groups of cetaceans may have been submerged as the survey vessel or aircraft transited past them (availability bias); other groups at the surface may have been missed by observers (perception bias). The proportion of acoustic detections that were also detected visually (62%) suggests that the magnitude of this latter bias is not large, especially given that some groups of vocalising dolphins may have been out of the detection range of visual observers. The first source of bias from aerial surveys was ameliorated by forcing survey type into the models and only predicting with the factor coefficient associated with vessels (this effectively forces the $g(0)$ estimate for aircraft no more negatively biased than that for ships). It might be expected that survey platform (Survey) should always naturally appear in the models, as $g(0)$ should generally be higher for a ship than a plane. This was not always the case due, in part, to the low power to detect this effect because of the low number of sightings. Thus, Survey was forced into the model for bottlenose dolphins.

Other researchers have used a variety of analytical approaches to estimate $g(0)$ directly. In vessel surveys of small delphinids (including the genera *Stenella* and *Tursiops*), Barlow and Forney (2006) estimated $g(0)$ to be 0.86 for groups of less than 20 individuals and 0.97 for groups of 20 or larger. In aerial surveys of bottlenose dolphins in California, Forney and Barlow, (1998) estimated a $g(0)$ of 0.67 for small (1–10) and 0.85 for large (>10) groups, although these values did not fully account for availability bias. Spotted and bottlenose dolphins in Onslow Bay occurred in a variety of group sizes and some groups on the trackline were not detected by our observers. Thus, the estimates of density and abundance estimates are negatively biased to an unknown degree.

**Assessment of field approach**

As noted above, the objective of the research was to provide a comprehensive description of the occurrence, distribution and abundance of cetaceans off Onslow Bay. A suite of complementary approaches were selected to ensure that the
presence of all cetaceans could be assessed and to maximise information collected by these different research modalities. Aerial surveys gave the advantage of relatively brief breaks in the weather, which was particularly important in winter, when survey conditions were generally poor. There have been few prior attempts to conduct regular surveys of cetaceans in the North Atlantic during winter. The surface vessels provided an independent means of assessing occurrence, distribution and abundance and, importantly, allowed investigation of patterns of residency using photo-identification methods. Merging results from the aerial and vessel surveys added a layer of complexity to the analysis, but this did not outweigh the benefit of the combined approach. Although not discussed here, the vessel surveys also allowed collection of biopsy samples that are important for studies of population structure and feeding ecology. Finally, our passive acoustic monitoring program allowed a continuous record of the presence of vocalising cetaceans in all seasons, weather conditions and during both day and night. The passive acoustic techniques also allowed determination of whether the visual surveys missed any deep-diving or cryptic species. This additional information indicated that at least some pygmy or dwarf sperm whales were present in Onslow Bay, but not detected during aerial or shipboard surveys. Despite the advantages of this complementary approach, however, the low encounter rates of cetaceans in Onslow Bay limit the statistical power with which it is possible to detect changes in density caused by anthropogenic or natural factors, given any reasonable level of survey coverage.

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